
LARVAL LABRISOMIDAE (PISCES: BLENNIOIDEI) FROM THE GALÁPAGOS ISLANDS

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ABSTRACT. Larval Labrisomidae from the Galápagos Islands are described from field-collected specimens. The species included are *Starksia galapagensis*, *Dialommus fuscus*, *Labrisomus dendriticus*, *L. multiporosus*, *Malacotenus tetranemus*, and *M. zonogaster*. Identifications were based on meristic data and on comparison of morphology between adults and larger larvae. Labrisomid larvae are elongate, slightly compressed, with 30–47 myomeres, head small and generally rounded with a short snout, external melanophores at anterior tip of the cleithral symphysis; at least one pair of melanophores on head; a ventral row of melanophores on tail (between pterygiophores of anal fin); melanophores above gut (visible only in early stages); and a large swimbladder that is lost during development. Characters that separate *S. galapagensis* larvae from other labrisomids are a more advanced development at smaller size and a longer preanal length (47–53% vs <45% of standard length). Larvae of *Dialommus fuscus* have a high number of dorsal spines (24–27), a high number of anal rays (26–28), a high number of vertebrae (43), and a short preanal distance (33% of standard length). *Labrisomus* and *Malacotenus* larvae have no obvious synapomorphies. Species are identified by particular combinations of characters: preopercular spines, and melanophores on the upper jaw, dorsal margin of trunk, hypural border, and urostyle. In late larvae, the relative size of spines and rays in the dorsal fin is useful in identification.

RESUMEN. Se describen las larvas de los labrisómidos de las Islas Galápagos, utilizando especímenes recolectados en terreno. Las especies consideradas son: *Starksia galapagensis*, *Dialommus fuscus*, *Labrisomus dendriticus*, *L. multiporosus*, *Malacotenus tetranemus*, y *M. zonogaster*. La identificación de las larvas se estableció en base a información merística y comparación de morfología de adultos con la de larvas de mayor tamaño. Las larvas de labrisómidos son elongadas, levemente comprimidas lateralmente, con 30–47 miómeros, tienen una cabeza pequeña y generalmente redondeada, con un hocico corto, con un melanóforo externo en el extremo anterior de la sínfisis de los cleitros, con un par (al menos) de melanóforos sobre la cabeza, con una hilera ventral de melanóforos en el margen ventral del cuerpo (entre los pterigióforos de la aleta anal), con melanóforos sobre el intestino (visibles solo en etapas tempranas), y una vejiga gaseosa grande que se pierde durante el desarrollo. Caracteres útiles en la separación de las larvas de *S. galapagensis* de las de otros labrisómidos son un desarrollo más avanzado a una talla más pequeña y una mayor longitud preanal (47–53% vs <45% de la longitud estándar). Las larvas de *Dialommus fuscus* tienen un alto número de espinas en la aleta dorsal (24–27), un alto número de radios anales (26–28), un alto número de vértebras (43), y una corta distancia preanal (33% de la longitud estándar). *Labrisomus* and *Malacotenus* no muestran obvias sinapomorfias larvales a nivel de género. Las especies se pueden identificar por combinaciones particulares de caracteres; espinas preoperculares, y melanóforos en premaxilar, margen dorsal del tronco, borde de las placas hipurales, y urostilo. En larvas más grandes, la estructura de la aleta dorsal, i.e. el tamaño relativo de espinas y radios es también útil en la identificación.

INTRODUCTION

Labrisomid blennies are small (5–12 cm), demersal reef and nearshore fishes, primarily of the New World. The group is represented by 98 species (14 genera), with approximately half of the species in the eastern Pacific (Nelson, 1984; Grove and Lavenberg, 1997).

Information about life history is available for some members of the family. Matarese et al. (1984) summarized briefly larval characters at a time when

not many larvae were described and the family was not well defined. More recent and more significant contributions include the works of Brogan (1992), who studied the larvae of several species of labrisomids and other blennies from the Gulf of California, and Watson (1996), who described the larvae of five species from the California Current Region.

We describe postflexion larvae of *Starksia galapagensis* (Rosenblatt and Taylor, 1971), *Dialommus fuscus* (Gilbert, 1891), *Labrisomus multiporosus* (Hubbs, 1953), *L. dendriticus* (Reid, 1935), *Malacotenus tetranemus* (Cope, 1877), and *M. zonogaster* (Heller and Snodgrass, 1903), based on field-collected specimens from the Galápagos Is-

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Table 1. Summary of meristic characters for the genera of eastern Pacific Labrisomidae.

Tribes/Genus	D	A	P1	P2	Vertebrae
Cryptotremiini					
<i>Alloclinus</i>	XXIV-XXVI, 9-11	II, 21-23	13-14	I, 3	41-42
<i>Auchenionchus</i>	XXIV-XXVI, 11-12	II, 21-24	13-14	I, 3	42-43
<i>Calliclinus</i>	XXIV-XXV, 11-13	II, 20-22	15	I, 4	41-43
<i>Cryptotrema</i>	XXVI-XXXVIII, 11-12	II, 24-27	—	I, 3	45-47
Labrisomini					
<i>Malacoctenus</i>	XIX-XXII, 9-13	II, 17-23	13-16	I, 3	36-45
<i>Labrisomus</i>	XVII-XX, 10-13	II, 16-20	13-16	I, 3	33-46
Mnierpini					
<i>Dialommus</i>	XXIV-XVII, 12-14	I, 26-27	13	I, 3	43
<i>Mnierpes</i>	XXI-XXIII, 10-12	II, 22-23	12-13	I, 3	39
Paraclinini					
<i>Exerpes</i>	(III-IV)-(XXIII-XXVI), 1/2	II, 17-20	13-15	0-I, 2-3	35
<i>Paraclinus</i>	XXVI-XXXIII, 0-1	II, 16-21	11-15	0-I, 2-3	33-39
Starksiiini					
<i>Starksia</i>	XIX-XXII, 7-10	II, 16-21	12-15	I, 3	30-35
<i>Xenomedeia</i>	XX-XXIII, 8-11	II, 18-22	12-14	I, 3	34-37

lands. The larvae of another labrisomid species that occurs in the Galápagos Islands, *L. jenkinsi* (Heller and Sodgrass, 1903) were not found in the samples. *M. tetranemus* and *L. multiporosus* range from the Gulf of California to northern Chile, whereas the other species, except *L. dendriticus*, are endemic to the Galápagos Islands. *L. dendriticus* is an eastern Pacific oceanic island endemic, known only from Isla Malpelo and the Galápagos Islands (Grove and Lavenberg, 1997).

MATERIALS AND METHODS

Plankton samples were collected by the R/V VELERO III during the Allan Hancock expedition cruises to the eastern tropical Pacific and Galápagos Islands. Most samples were collected during 1933; however, a few specimens came from the expeditions of 1932 and 1934. The collections were made at night (at anchorage), using an electric light and dipnets. Sampling sites were mainly at Española, Santa Maria, Santa Cruz, Isabela, Baltra, and Genovesa Islands (Fraser, 1943).

The specimens (preserved in 70% ethanol) were sorted from the larval fish collections at the Natural History Museum of Los Angeles County (LACM). Specimens were identified by the size-series method (Powles and Markle, 1984), relying on the diagnostic meristics of each species. Meristic data were obtained from Hubbs (1952, 1953), Rosenblatt and Taylor (1971), Springer (1959), Stephens and Springer (1973), Brogan (1992), and Hastings and Springer (1994). Additional vertebral counts and fin meristics were obtained from radiographs of juvenile and adult specimens from the LACM holdings.

All measurements, standard length (SL) and preanal length, were recorded to the nearest 0.1 mm using a Wild M3 stereomicroscope. A representative size series of each species, when available, was illustrated with the aid of a camera lucida. Brief descriptions are given for species represented by a few larvae; they are usually about the same

size (e.g., *Dialommus fuscus*). Meristic data from radiographs of specimens, combined with data from the literature (for labrisomid genera and species from the Galápagos Islands), are summarized in Tables 1 and 2.

LABRISOMIDAE

The Labrisomidae are teleostean fishes of the sub-order Blennioidei, which are considered to be paraphyletic on the basis of DNA sequences and allozyme data (Stepien, Dixon, and Hillis, 1993). Springer (1993) found no evidence to support the monophyly of the Labrisomidae among the 34 characters he analyzed across all the Blennioidei. Stepien et al. (1997) recently hypothesized that the group composed of the Labrisomidae, Clinidae and Chaenopsidae is monophyletic. The paraphyly in the Labrisomidae is probably due to the inclusion of some genera based on plesiomorphic characters such as the presence of a scaled body and a lateral line (Hastings and Springer, 1994).

Currently the labrisomids include 14 genera, allocated into five tribes, and are diagnosed by a dorsal fin either entire or in a spinous and segmented ray portion with more spines than segmented rays, 17–33 dorsal-fin spines, 0–13 simple segmented dorsal-fin rays (never branched), two anal-fin spines (except for *Dialommus* with one), 16–27 segmented anal-fin rays, pectoral-fin rays unbranched, scales cycloid when present with radii only in anterior field, free bony margins of opercular bones not fimbriate, no projection of the pelvic girdle extending anteriorly in front of the juncture with the cleithra, pelvic fins insert in advance of the pectoral fins, dorsal- and anal-fin rays equal in number to the vertebrae between them, and more than 30 vertebrae (see Springer, 1993 for additional labrisomid

Table 2. Summary of meristic and relevant morphologic data for larval Labrisomidae found in the Galápagos Islands. From Hubbs (1952, 1953); Rosenblatt and Taylor (1971); Springer (1959); Stephens and Springer (1973); and this study.

Species	Vertebrae	Dorsal*	Anal*	Pectoral*	Pigmentation				Preopercular spines	Preanal distance
					D	UJaw	Hyp	Uro		
<i>Starksia galapagensis</i>	34–35	XX–XXI (XXII) 7–10	II, (16) 17–19	13–14	–	–	–	–	–	47–53
<i>Dialommus fuscus</i>	43	XXIV–XXVII, 10–13(14)	I, 26–28	13	–	–	+	–	–	33
<i>Labrisomus dendriticus</i>	36	XX, (10) 11–12	II, (19) 20–21	13	+	+	+	–	+	40–45
<i>Labrisomus jenkinsi</i>	–	XXVII–XIX, 10–11	II, 17	14–15	?	?	?	?	?	?
<i>Labrisomus multiporosus</i>	34–35	(XVII–XIX) 11–13	II, (17–19)	(13–15)	+	–	+	+	+	41–46
<i>Malacotenus tetranemus</i>	35–36	(XVIII–XX) 10–12	II, 18–20	(13–15)	+	+	–	–	+	41–45
<i>Malacotenus zonogaster</i>	37–38	XXI–XXII, 10–11(12)	II, (19) 20–21	14	+	+	+	+	–	38–41

Abbreviations: * Counts in parentheses are less frequent; ranges in parentheses indicate that both extreme values are less frequent; underscored are most frequent counts. Pigmentation: melanophore presence (+) or absence (–) dorsally (D) on the body (c, continuous row of melanophores), UJaw (upper jaw, number in parentheses), Hyp (hypural), Uro (urostyle; D, dorsal; L, lateral); Preopercular spines: presence (+) or absence (–); preanal distance expressed as a percentage of standard length. Meristic data for *Labrisomus jenkinsi* are provided only for reference, as the larvae remain undocumented.

features). These fishes are restricted to the tropical and warm temperate waters of the New World and the west coast of Africa (see Stepien 1992, figure 1; we cannot verify the western Pacific record shown in figure 1).

Labrisomids have two modes of spawning; ovoviviparity in the tribe Starksini and oviparity in the other four tribes. In the Starksini the first anal-fin spine is modified into an elongate genital papilla to serve as an intromittent organ. Development proceeds in the follicles of the ovary, and the embryos hatch at an advanced larval stage. To our knowledge, all other labrisomids exhibit some degree of courtship and spawn adhesive demersal eggs into a nest site, which is guarded by the parents. At hatching, larvae have pigmented eyes and measure about 3–4 mm notochordal length (NL). Notochord flexion usually occurs shortly thereafter.

Larvae are elongate, slender, and slightly laterally compressed with at least 30–47 myomeres; gut initially straight, preanal length usually less than 50% of standard length, up to 53% in *Starksia*; a large swimbladder (absent in adults); a small, rounded head; a short snout; six branchiostegal rays; and 7+6 principal caudal rays. Pigmentation is weak or light; melanophores occur primarily on dorsal cranial surfaces; on the nape; anterior to the gut, behind the cleithra; over the swimbladder; at the tip of the cleithral symphysis; on the hind gut; and along the ventral margin of the tail, especially between the pterygiophores of the anal-fin rays. Labrisomid larvae show no pronounced morphological specializations to pelagic life.

LARVAL DESCRIPTIONS

Starksia galapagensis (Rosenblatt and Taylor, 1971)

Figure 1

GENERAL MORPHOLOGY. Based on 237 specimens, larvae and juveniles (11.6 to 14.2 mm). *Starksia galapagensis* has single nasal, orbital, and nuchal cirri and no preopercular spines (Table 2). The smallest specimen (Fig. 1a, 11.6 mm) has completed notochord flexion. No significant changes in body shape occur during subsequent development (Fig. 1a–c). The largest larva was 14.2 mm (Fig. 1c), although metamorphosing specimens were slightly smaller (Fig. 1d–e). By 12.4 mm, all the pores of the circumorbital series (10), and three in the preoperculo-mandibular series (Fig. 1d) are developed.

FIN DEVELOPMENT. All fin spines and rays are present at 11.6 mm. The shape and relative proportions of spines and rays are constant, except for the posteriormost three to four anal-fin rays that grow longer than the rest, forming a lobe nearly as long as the caudal peduncle.

PIGMENTATION. Larval *Starksia galapagensis* are unique in having a large ventral melanophore on the surface of the basipterygium. A single small melanophore may develop on the ventral margin of

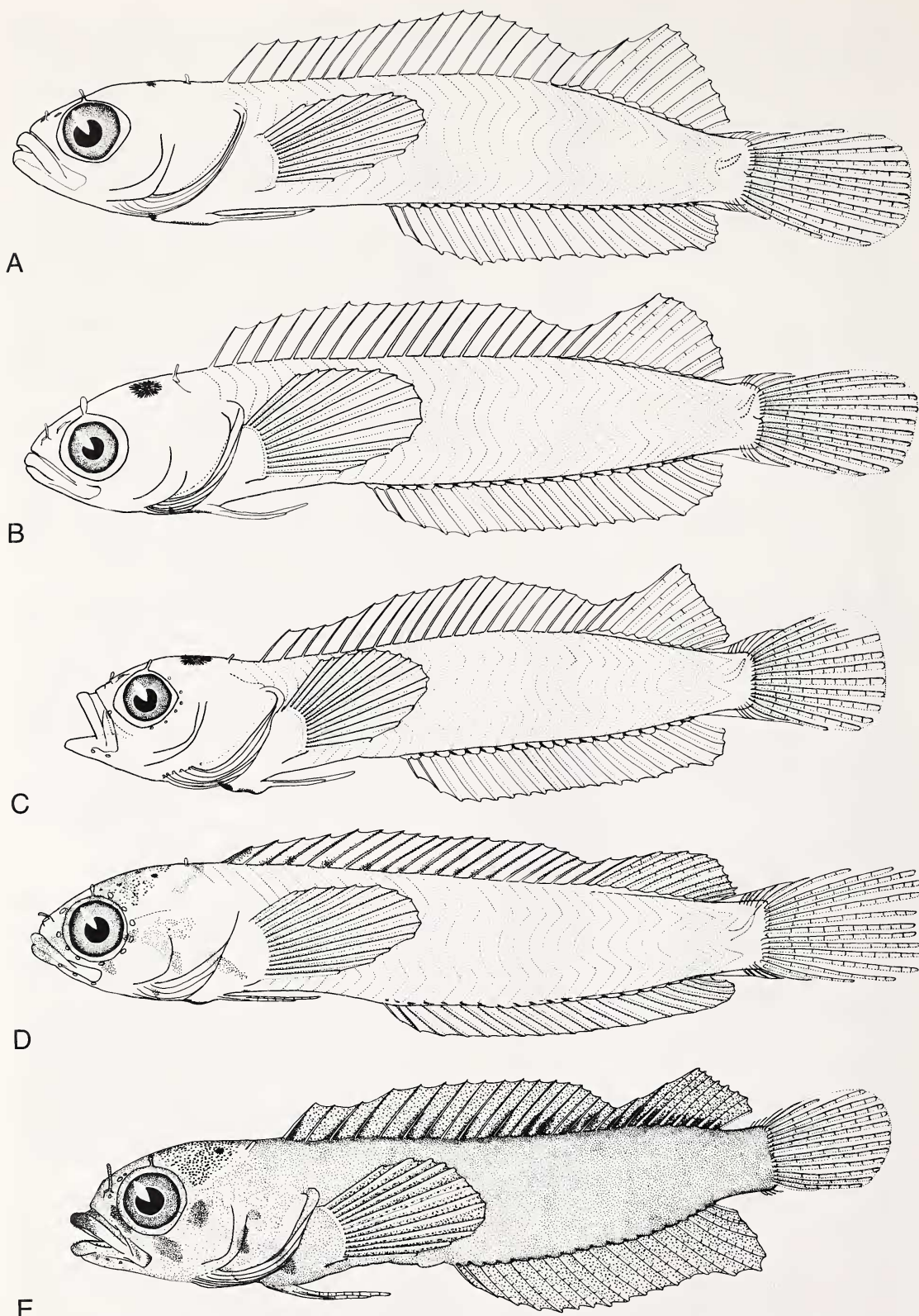


Figure 1. Field collected larvae and juvenile of *Starksia galapagensis*: (a) 11.6-mm larva (LACM 45644-12), (b) 13.0-mm larva (LACM 45663-13), (c) 14.2-mm larva (LACM 45621-20), (d) 12.4-mm transforming specimen (LACM 45634-15), (e) 12.6-mm juvenile (LACM 43688-1).

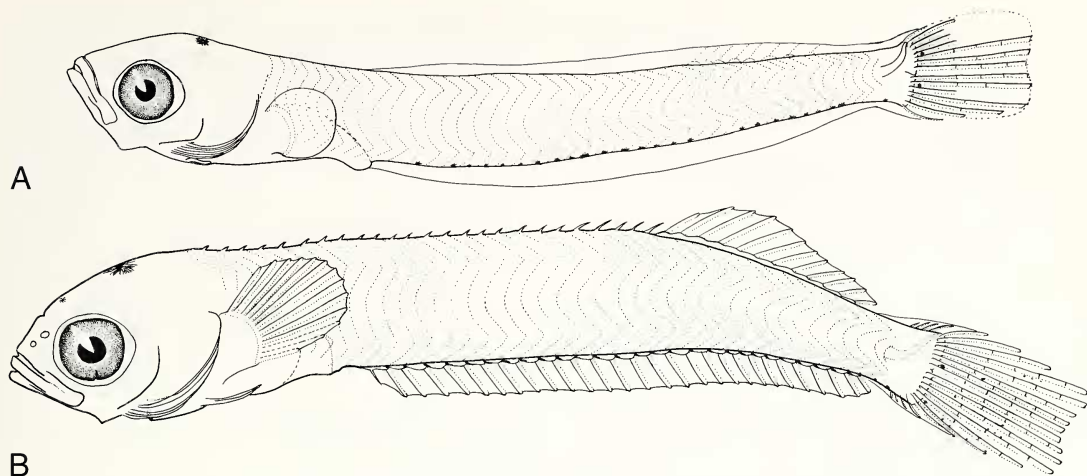


Figure 2. Field collected larvae of *Dialommus fuscus*: (a) 8.4 mm (LACM 45665-2), (b) 10.2 mm (LACM 45621-14).

the caudal peduncle. The 12.4-mm specimen (Fig. 1d) seems to be in the process of metamorphosis; this specimen also has a small melanophore ventral to the gut, at the pectoral-fin base level.

Part of the typical dark spots, composed of small melanophores and observed in the head of the adults, can be recognized in the two larger specimens; these spots are in lips; in front of, below and behind the eye; in the operculum; and in front of the pectoral fins (Fig. 1d-e).

At metamorphosis, small melanophores develop along the anterior and posterior margins of all fin spines and rays. Furthermore, there are blotches in the dorsal fin membrane with higher concentration of melanophores. In older specimens (Fig. 1e), small punctate melanophores develop on the entire body and fins; those dorsally on the head are a little larger. The ventral melanophore on the basipterygium is also lost.

REMARKS. Among the six Galápagos labrisomids, only *Starksia galapagensis* has fully developed larvae at sizes as small as 11.6 mm and metamorphic specimens smaller than 14 mm. Distinctive characters are the elongate melanophore ventrally on the basipterygium and a preanal length >47% standard length (SL).

Dialommus fuscus (Gilbert, 1891)

Figure 2

GENERAL MORPHOLOGY. Description based on 13 specimens; two larvae (8.4 and 10.2 mm) described in detail. Compared with the other known larval Galápagos labrisomids, the larvae of this species are more slender, with a shorter preanal length (Table 2). Neither specimen has developed cirri. There are no preopercular spines, and apparently they are absent in all larval *Dialommus*.

FIN DEVELOPMENT. Flexion and caudal-fin ray development are complete at 8.4 mm, and the

dorsal-fin pterygiophores are developing posteriorly (Fig. 2a). At 10.2 mm, dorsal- and anal-fin spines and rays are present, but most of the dorsal-fin spines are poorly developed. Pectoral-fin rays are not completely formed (Fig. 2b).

PIGMENTATION. Two well-separated melanophores develop on the principal caudal-fin rays near the distal margins of the upper and lower hypural plates but not in contact with them. A pair of small melanophores develops in the interorbital region anterior to the two large cephalic melanophores at 10.2 mm (Fig. 2b). Three small melanophores can be found on the ventral margin of the caudal peduncle.

REMARKS. Larvae of *D. fuscus* can be identified by a long and slender body shape, a short preanal distance, high myomere count (43), and distinctive caudal-fin melanophores. In late larvae, the number of spines and rays in the dorsal and anal fins is diagnostic (Table 2).

Labrisomus dendriticus (Reid, 1935)

Figure 3

GENERAL MORPHOLOGY. Based on 176 larvae (6.4–22.7 mm). Body is elongate with a shape intermediate between the slender *Dialommus fuscus* and the more robust *Starksia galapagensis*. Slope of the head is flat in early stages (Fig. 3a), becoming more rounded (Fig. 3e). Preanal length ranges from 40–45% SL. Cirri develop later than in the other species of *Labrisomus* and *Malacotenus*. At 18.1 mm, nasal and orbital cirri are small buds (Fig. 3d). By 22.7 mm, bifid nasal and orbital cirri and three nuccal cirri are present (Fig. 3e); the nuccal cirri are smaller in *L. dendriticus* than in *L. multiporosus* and *Malacotenus*.

FIN DEVELOPMENT. At 6.4 mm, a full complement of anal-fin rays are developing, and the dorsal-fin anlage is formed. Dorsal-fin spines begin

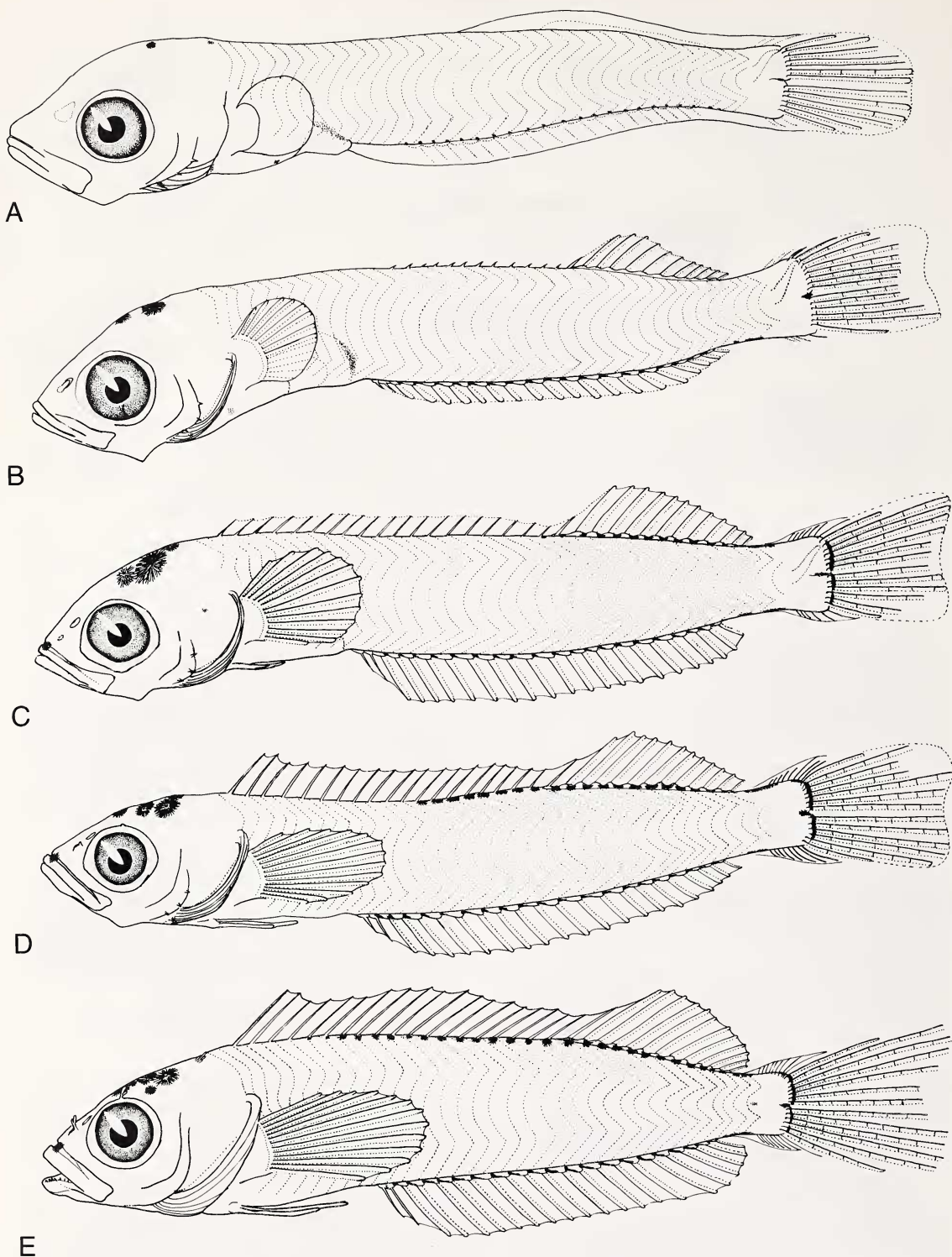


Figure 3. Field collected larvae of *Labrisomus dendriticus*: (a) 6.4 mm (LACM 45656-3), (b) 8.4 mm (LACM 45614-4), (c) 13.6 mm (LACM 45614-4), (d) 18.1 mm (LACM 45614-4), (e) 22.7 mm (LACM 45621-5).

to develop posteriorly by 8.4 mm; all spines are formed by 13.0 mm. By 18.1 mm, the first two dorsal-fin spines are longer (Fig. 3d), as in adults.

SPINATION. Preopercular spines are developed by 6.4 mm (Fig. 3a). They become embedded in late-stage larvae and remain visible to at least 18.1 mm; they disappear by 22.7 mm (Fig. 3e).

PIGMENTATION. The most distinctive character is the presence of a melanophore between the hypural plates, close to the posterior border (Fig. 3a). A pair of melanophores develops on the upper jaw at about 9.0 mm. A single pair of melanophores is present above the midbrain in larvae <7.0 mm, increasing to three pairs in larvae >16.0 mm (Fig. 3a–d). At 6.4 mm, a ventral melanophore is present on the gut (Fig. 3a), but it disappears before 8.4 mm.

At about 10 mm, two melanophores develop behind the distal hypural margins. Two to four melanophores are present on the ventral margin of the caudal peduncle (Fig. 3a, 6.4 mm); one to two melanophores develop on the dorsal margin after 10.0 mm (Fig. 3c–e). A continuous row of melanophores develops along the pterygiophores of the dorsal fin, spreading both caudad and cephalad from the anterior soft rays, beginning at 10.2 mm; in the largest specimen, this row extends from the fourth or fifth spine to the last dorsal-fin ray (Fig. 3e). At 22.7 mm, external melanophores form laterally on the caudal peduncle (Fig. 3e), probably signaling the beginning of metamorphosis.

REMARKS. Of the six species studied, *Labrisomus dendriticus* is the only one that has a melanophore between the hypural plates and a continuous dorsal row of melanophores on the trunk and tail. Other distinguishing characters are small nuchal cirri; presence of preopercular spines; a pair of melanophores on the upper jaw; and a series of melanophores along the posterior border of the hypural plates. Also, *L. dendriticus* develops one or two melanophores on the dorsal margin of the caudal peduncle, a feature that is absent in larvae of *L. multiporosus*.

The two species of *Labrisomus* have the same configuration of spines and rays in the dorsal fin. The terminal dorsal-fin spine is longer than the preceding spines and superficially appears to be part of the segmented ray portion of the dorsal fin. *Malacotenus* differs from *Labrisomus* in that the last two dorsal-fin spines are longer than the preceding ones and appear to belong to the segmented ray portion of the fin.

Labrisomus multiporosus (Hubbs, 1953)

Figure 4

GENERAL MORPHOLOGY. Based on 915 larvae (5.4–18.4 mm). These larvae are morphologically similar to those of *L. dendriticus*. The largest specimen, 18.4 mm, has bifid nasal cirri, a single orbital cirri, and five nuchal cirri of moderate length (Fig. 4f). A diagnostic feature of adults is a complex

cranial pore pattern, which begins to develop in late-stage larvae. Pores form above the eye by 14 mm and proliferate as development proceeds, particularly around the orbit and laterally on the lower jaw (Fig. 4e–f).

FIN DEVELOPMENT. The development of dorsal and anal fins is similar to that of *L. dendriticus*. At 5.4 mm, only part of the dorsal-fin anlage is present, and notochord flexion is complete. At 7.2 mm, dorsal and anal fins are partially formed. By 14.5 mm, the anteriormost four dorsal-fin spines are of about uniform length (Fig. 4e–f), resulting in the characteristic straight fin margin.

SPINATION. Three preopercular spines are present in small larvae (5.4 mm), and the number increases to four spines by 14.5 mm (Fig. 4e) and to 8 at 18.4 mm (Fig. 4f). The spines are not lost, as occurs in other species; the adults of *L. multiporosus* are characterized by the presence of preopercular spines.

PIGMENTATION. Melanophores develop between the pterygiophores of the first three segmented dorsal-fin rays at 11 mm (Fig. 4d). They spread cephalad in a discontinuous row to the seventh or eighth spine, and they spread caudad in a continuous row to near the last ray.

Internal melanophores develop laterally on the urostyle (Fig. 4e–f), and a series of external melanophores develops along the posterior margin of the hypurals (Fig. 4a) in larvae as small as 5.4 mm. At 14.5 mm, a few small punctate melanophores pepper the caudal fin membrane, mainly in the lower lobe (Fig. 4e). Two to five melanophores are present on the ventral margin of the caudal peduncle; these may coalesce, and by 18.4 mm, only two large melanophores can be discerned (Fig. 4f).

Melanophores above the brain increase from one pair at 5.4 mm to two pairs at 7.2 mm (Fig. 4a–b) and to three pairs at 14.5 mm, with the appearance of progressively more anterior pairs (Fig. 4e–f). At 5.4 mm, there is one ventral melanophore on the gut and two below the anus; all of these disappear before 7.2 mm (Fig. 4b). At 18.4 mm, three large melanophores form ventrally on the gut and one forms ventrolaterally below the pectoral base (Fig. 4f).

REMARKS. Among the six Galápagos labrisomid species, *L. multiporosus* is the only one that retains preopercular spines as a juvenile. Furthermore, the number and size of spines increase in larger larvae.

In contrast to *L. dendriticus*, *L. multiporosus* lacks melanophores on the upper jaw and between the hypural plates. Further, the development and number of preopercular spines, the dorsal pigment pattern, and the size of dorsal-fin spines and rays serve to distinguish these two species. The two species show differences in the time of development of pigment along the hypural margin: in *L. multiporosus* melanophores develop early (by 5.4 mm), whereas in *L. dendriticus* they develop late (by 10 mm).

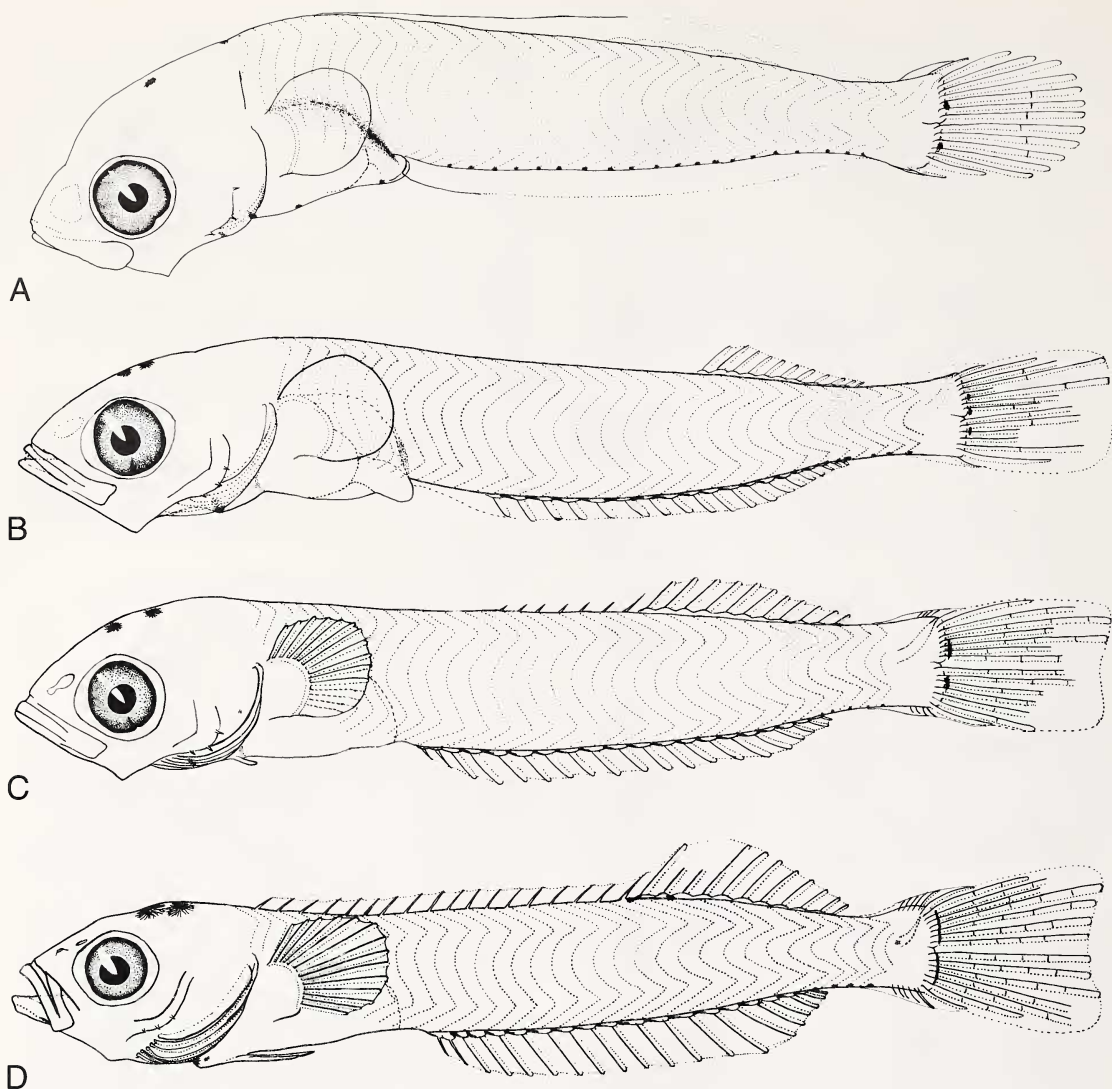


Figure 4. Field collected larvae of *Labrisomus multiporosus*: (a) 5.4 mm (LACM 45623-5), (b) 7.2 mm (LACM 45675-4), (c) 8.3 mm (LACM 45675-4), (d) 11.8 mm (LACM 45621-6), (e) 14.5 mm (LACM 45623-5), (f) 18.4 mm (LACM 45623-5).

Malacoctenus tetranemus (Cope, 1877)

Figure 5

GENERAL MORPHOLOGY. Based on 228 larvae (5.4–17.3 mm). The larval shape as in other *Labrisomus* and *Malacoctenus* species. Preanal length ranges from 41–45% SL. *M. tetranemus* develops six long nuchal cirri, a bifid nasal cirrus, and a bifid orbital cirrus. Two mandibular pores develop laterally on the lower jaw in larger specimens (Fig. 5d–e).

FIN DEVELOPMENT. Dorsal-fin spines begin to develop at 9.0 mm. By about 16 mm, the spinous dorsal fin is notched near its anterior and posterior ends (Fig. 5d–e). In *Malacoctenus*, the first two elements of the posteriorly lobed portion of the dor-

sal fin are spines. This feature is established by 10.2 mm in *M. tetranemus*, even before dorsal-fin spine development is complete (Fig. 5 b–e).

SPINATION. At 5.4 mm, *Malacoctenus tetranemus* has three preopercular spines (Fig. 5a); however, these disappear during development and are no longer visible in larvae larger than 16 mm (Fig. 5d–e).

PIGMENTATION. A pair of melanophores develops on the premaxillary in larvae as small as 5.4 mm (always present after 6.2 mm). Two pairs of melanophores develop on the midbrain before 7.0 mm, and by 12.2 mm, two additional pairs have appeared above the forebrain. These melanophores increase in size with development (Fig. 5c–e).

A row of melanophores appears between the

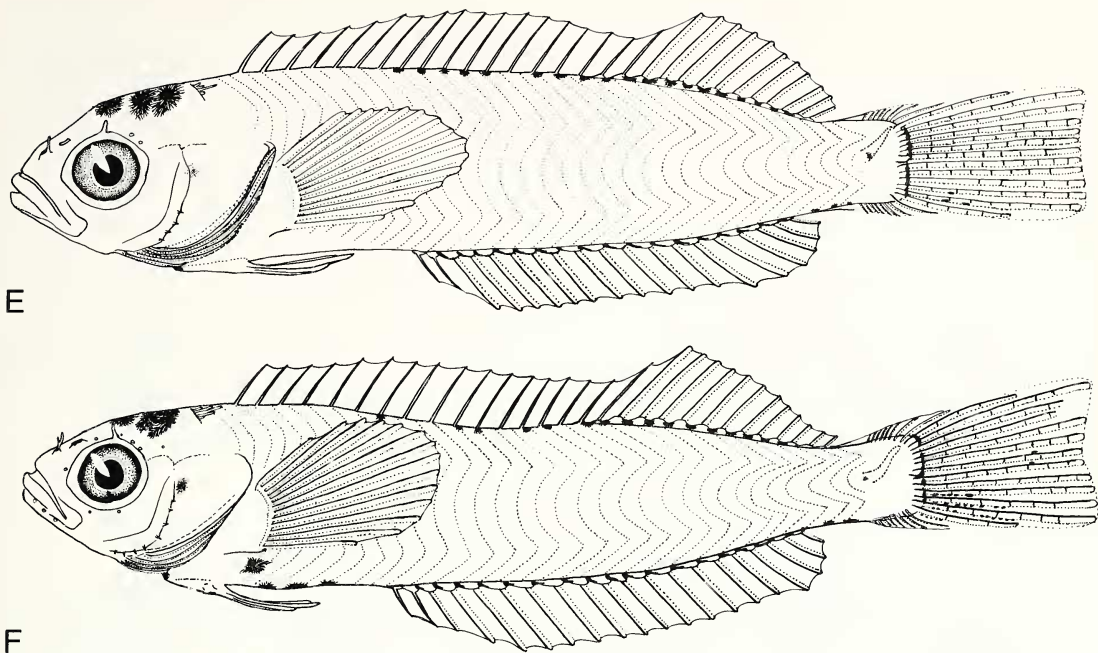


Figure 4. Continued.

first pterygiophores of the segmented ray portion of the dorsal fin by 10.2 mm (Fig. 5c) and subsequently spreads both cephalad and caudad (Fig. 5d–e). These melanophores are not arranged in a continuous row, nor is their position on the pterygiophores constant among individuals (Fig. 5d–e).

In larvae shorter than 7.0 mm, there is usually no pigmentation on the ventral margin of the caudal peduncle, but one small melanophore is present in some specimens. Two melanophores are present ventrally along the gut but disappear early by 10.2 mm (Fig. 5a). Melanophores typically are absent along the hypural margin.

REMARKS. Among the six species treated here, *M. tetranemus* has the largest and most numerous (6) nuccal cirri. It is easily distinguished from other species by the combination of preopercular spines, the absence of pigmentation along the hypural margin, and the presence of melanophores on the upper jaw. Further, *M. tetranemus* typically shows heavier cranial pigmentation.

Malacoctenus zonogaster (Heller and Snodgrass, 1903)

Figure 6

GENERAL MORPHOLOGY. Based on 414 larvae (7.0–17.7 mm). Preopercular spines are absent. Preadrenal length ranges from 39–41% SL. *Malacoctenus zonogaster* develops a single orbital cirrus, a bifid nasal cirrus, and three small nuccal cirri.

FIN DEVELOPMENT. Notochord flexion is

complete and segmented dorsal- and anal-fin rays are forming by 7.0 mm (Fig. 6a). Dorsal-fin spines begin to appear by 11.0 mm, and by 15.6 mm the typical adult pattern of having the first two dorsal-fin spines longer than the third and fourth spines is present (Fig. 6d–e). The generic character of having the last two dorsal-fin spines included in the segmented ray portion of the dorsal fin is present at 12.2 mm (Fig. 6d).

PIGMENTATION. Cranial pigment consists of a pair of melanophores on the frontals; another, larger pair on the parietals; and an embedded melanophore on the nape. A few smaller melanophores sparsely scattered on the head increase in number with growth (Fig. 6a–e).

A discontinuous row of melanophores develops between the anterior pterygiophores of the segmented ray portion of the dorsal fin at 12.2 mm and spreads cephalad to the fifth dorsal-fin spine and caudad (Figs. 6d–e), but not as far as the last two segmented rays. Larvae larger than 15 mm have a single, small, usually faint melanophore on the upper jaw. In contrast, other labrisomids with upper jaw pigment typically have a pair of melanophores.

A series of two to four melanophores appears on the ventral margin of the caudal peduncle after 7.0 mm (Fig. 6a), and this increases to four to six melanophores after 9.0 mm (Fig. 6b–e). On the dorsal peduncle margin, one or two melanophores develop at about 10.0 mm and are retained in later larval stages (Figs. 6b–e). Internal dorsal melano-

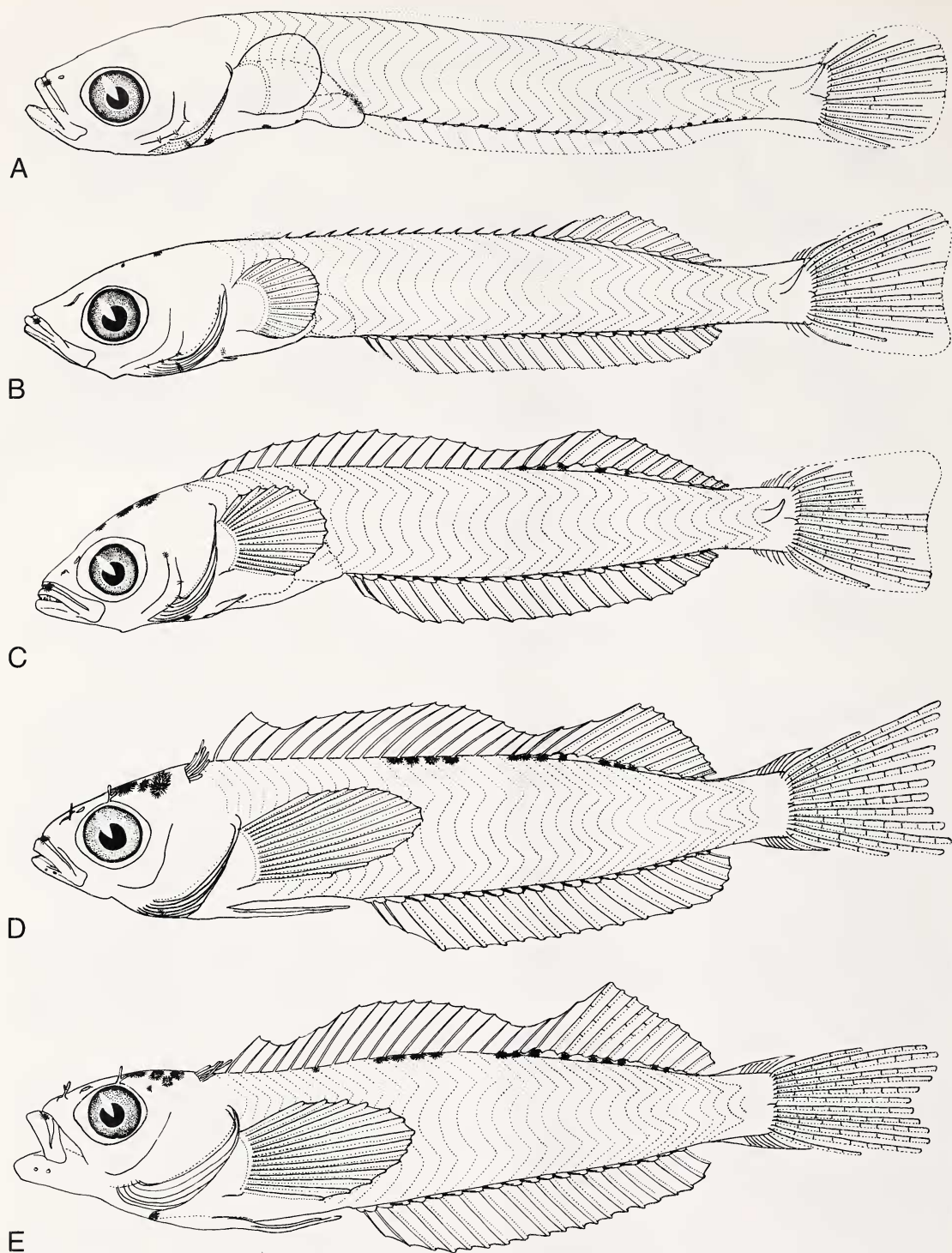


Figure 5. Field collected larvae of *Malaccoctenus tetranemus*: (a) 7.2 mm (LACM 45675-6), (b) 10.2 mm (LACM 45675-6), (c) 12.2 mm (LACM 45623-7), (d) 16.1 mm (LACM 45643-5), (e) 17.3 mm (LACM 45625-14).

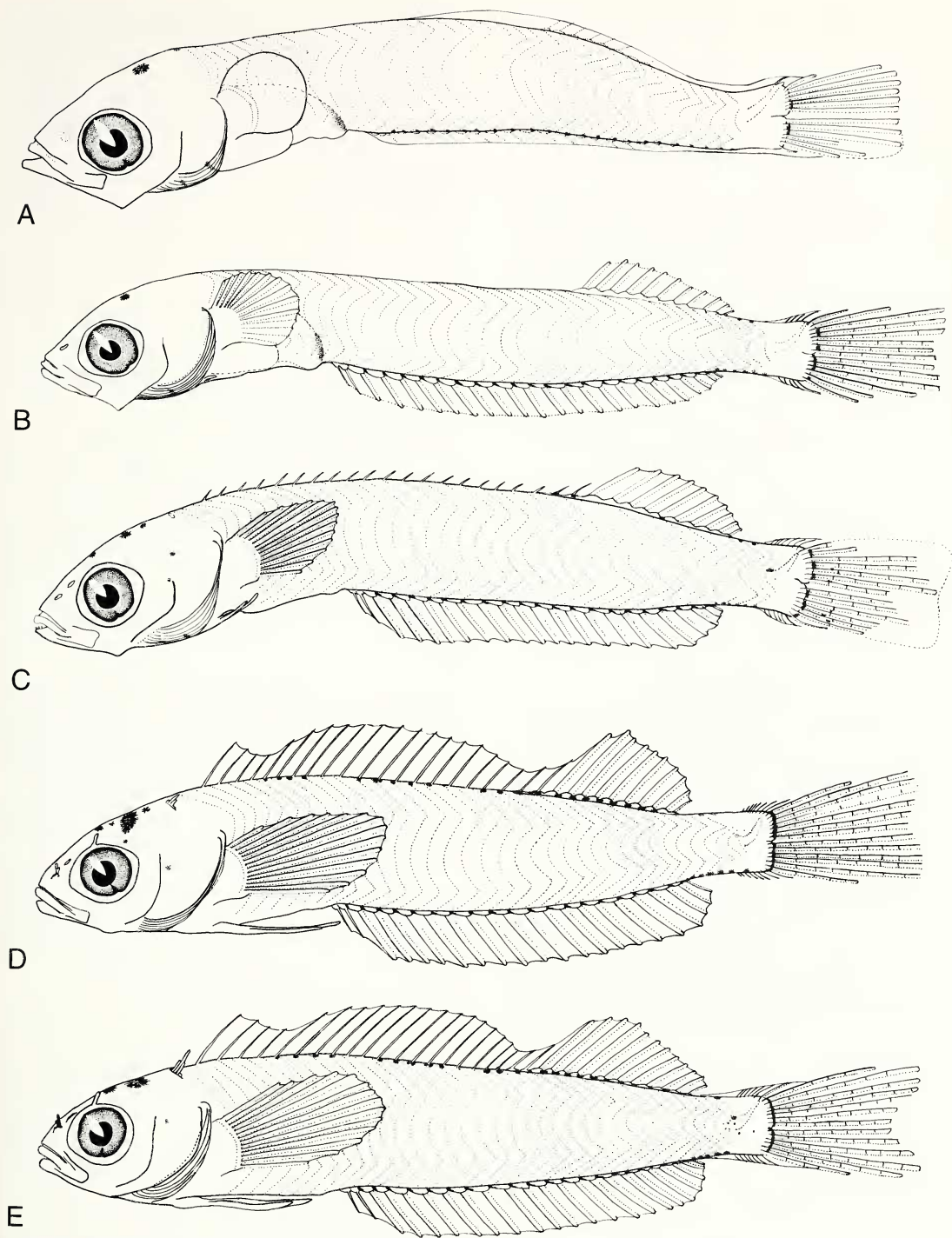


Figure 6. Field collected larvae of *Malacoctenus zonogaster*: (a) 7.0 mm (LACM 45675-7), (b) 10.2 mm (LACM 45675-7), (c) 12.2 mm (LACM 45623-7), (d) 15.6 mm (LACM 45625-15), (e) 17.7 mm (LACM 45622-2).

phores associated with the urostyle are present in larvae larger than 9.0 mm (Fig. 6c–e). Hypural border pigmentation is present by 7.0 mm, initially as one melanophore on the margin of each plate. These increase in number and eventually overlap, covering the entire hypural margin (Fig. 6d–e). At 18.4 mm, small melanophores develop on the lower caudal rays (Fig. 6e).

REMARKS. Both species of *Malacotenus* develop pigmentation on the upper jaw, but *M. zonogaster* has a single medial melanophore that develops late (>15.0 mm), whereas *M. tetranemus* has two that appear early (<6.0 mm SL). *M. zonogaster* also differs from *M. tetranemus* in lacking preopercular spines, in retaining the dorsal and ventral pigmentation on the caudal peduncle throughout larval life, and in having melanophores between nearly all pterygiophores on the segmented-ray portion of the dorsal fin, a pigmented hypural border, smaller nuchal cirri, and a single orbital cirrus.

Those larvae of *M. zonogaster* that lack dorsal-fin spines resemble the triplefin blenny, *Lepidoneustes corallicola* (Tripterygiidae). They can be distinguished from one another by the relative distance between the snout and the origin of the soft portion of the dorsal fin; this distance is 68–71% of SL in *M. zonogaster* and 60–63% in *L. corallicola*.

DISCUSSION

Even though the coverage here is limited both in number of species and stages of development examined, three larval types can be recognized according to their shapes, which coincide with traditional labrisomid classification. For example, a typical feature is the preanal distance, which reaches 38–46% in species of *Malacotenus* and *Labrisomus* (Labrisomini), 47–53% in *Starksia* (Starksini), and 33% in *Dialommus* (Mnierpini).

The larvae of *Starksia galapagensis* are morphologically different from those of other labrisomids, an observation that would be consistent with excluding the tribe Starksini from the family Labrisomidae. Based on molecular evidence, the tribe has been considered to be more closely related to Clinidae (Stepien et al., 1993) or Chaenopsidae (Stepien et al., 1997). The presence of a large and elongated ventral melanophore at the basipterygium in *S. galapagensis*, a striking feature of larval chaenopsids (Brogan, 1992), suggests a close relationship with the family Chaenopsidae.

The larvae of *Dialommus fuscus* differ from others in this study in having a more elongate body with a short preanal length (33%), a high number of vertebrae (43), pigmented hypural plate margins, a high number of spines in the dorsal fin (24–27), and a high number of rays in the anal fin (26–28). More comparisons are not possible because the available larvae of this species were few and the size range was narrow.

The species of *Labrisomus* and *Malacotenus* show specific arrays of preopercular spines and me-

lanophores on the upper jaw, dorsal margin of the trunk, hypural plate border, and urostyle. In larger larvae, the relative size of the first spines of the dorsal, and the number of spines included in the second lobe of the dorsal fin are helpful in identification. There are no characters that define *Labrisomus* and *Malacotenus* as early larvae. However, in larger specimens, an adult feature develops: the posterior lobe of the dorsal fin includes one spine in *Labrisomus* and two spines in *Malacotenus*.

Watson (1996) described larvae of *L. multiporosus* in the size range from 5.5–12.3 mm from the California Current Region, which differ in some aspects with those from the Galápagos. These larvae develop several relatively large melanophores around the gut early in their development, whereas larvae from the Galápagos do not have them in the same size range. Some can be seen after 14.5 mm, but this seems to be more a juvenile feature. Furthermore, at the same stage of development, the larvae of *L. multiporosus* from the Galápagos have fewer preopercular spines than their counterparts from the California Current Region. It remains to be determined whether these differences are due to variation within the same species, which has an extended geographic range in the Eastern Pacific, or whether a separate species is present in the Galápagos.

Brogan (1992) described larvae of two species of *Labrisomus* (not identified) from the Gulf of California, with one to three large ventral melanophores ventrally on the trunk and no preopercular spines. Watson (1996) reports the same for *L. xanti*. A generalized pattern for blennioids is the presence of a continuous series of melanophores associated with the bases of the anal fin elements (Cavalluzzi, 1997), as it occurs in the two species from the Galápagos illustrated in this study. Then, the pigment pattern shared by the larvae of the three species described by Brogan (1992) and Watson (1996) would represent a derived condition suggesting a closer relationship among them.

Brogan (1992) described the larvae of two species of *Malacotenus* and found that one of them, *M. hubbsi*, never develops preopercular spines. Because this character is generalized in *Malacotenus* (and *Labrisomus*), its absence suggests a closer relationship between *M. hubbsi* and *M. zonogaster*. The knowledge of the larvae of *Malacotenus* and *Labrisomus* is still limited. For each of these two genera, there are about nine species in the eastern Pacific and nine in the western Atlantic. With the larvae of only five species of each genus known so far, any generalization about relationships based on ontogenetic characters is still speculative.

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